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Advancing research on alien species and biological invasions

Food-web modification in the eastern Gulf of Finland after invasion of *Marenzelleria arctia* (Spionidae, Polychaeta)

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Abstract

The paucity of data on non-indigenous marine species is a particular challenge for understanding the ecology of invasions and prioritising conservation and research efforts in marine ecosystems. *Marenzelleria* spp. are amongst the most successful non-native benthic species in the Baltic Sea during recent decades. We used stable isotope analysis (SIA) to test the hypothesis that the dominance of polychaete worm *Marenzelleria arctia* in the zoobenthos of the Neva Estuary after its invasion in the late 2000s is related to the position of this species in the benthic food webs. The trend towards a gradual decrease in the biomass of *Marenzelleria* worms was observed during 2014–2020, probably due to significant negative relationships between the biomass of oligochaetes and polychaetes, both of which, according to SIA, primarily use allochthonous organic carbon for their production. The biomass of benthic crustaceans practically did not change and remained very low. The SIA showed that, in contrast to the native crustacean *Monoporeia affinis*, polychates are practically not consumed either by the main invertebrate predator *Saduria entomon*, which preys on *M. affinis*, oligochaetes and larvae of chironomids or by benthivorous fish that prefer native benthic crustaceans. A hypothetical model for the position and functional role of *M. arctia* in the bottom food web is presented and discussed. According the model, the invasion of *M. arctia* has created an offshoot food chain in the Estuary food webs. The former dominant food webs, associated with native crustaceans, are now poorly developed. The lack of top-down control obviously contributes to the significant development of the *Marenzelleria* food chain, which, unlike native food chains, does not provide energy transfer from autochthonous and allochthonous organic matter to the upper trophic levels. The study showed that an alien species, without displacing native species, can significantly change the structure of food webs, creating blind offshoots of the food chain.

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Keywords
NIS, stable isotopes, bioturbation, detritivores, macroinvertebrates, zoobenthos, Neva Estuary

Introduction

Biological invasions are widely recognised as a key component of current global change. Human livelihoods and well-being in almost all regions of the world depend on alien taxa (Kumschick et al. 2020). Recently, the effects of invasive species may be exacerbated due to climate change (Moritz and Agudo 2013; Holopainen et. al. 2016; Golubkov 2021). For example, the expected rise in water temperature in the northern part of the Baltic Sea may lead to frequent invasions and spread of the more thermophilic Ponto-Caspian species in this region (Holopainen et. al. 2016). In addition, ever-increasing shipping raises the probability of introduction of alien species from any region. The paucity of data on non-indigenous marine species (NIS) is a particular challenge for understanding the ecology of invasions and prioritising conservation and research efforts in marine ecosystems (Ojaveer et al. 2015). Some NIS may have economic consequences on fisheries and the tourism industry and can result in substantial monetary costs and/or alterations to entire ecosystems and social systems (Kumschick et al. 2012, 2015; Galil et al. 2014; Ojaveer et al. 2015). Therefore, monitoring for the presence of impacting alien species is a requirement for the management of marine environment (Lehtiniemi et al. 2015).

Amongst the other approaches, food webs, which describe the trophic links amongst species in a system, are particularly important for studying the impacts of invasions (David et al. 2017). For instance, invasion can trigger a trophic cascade, affecting the abundance of the main trophic groups in the food web (Penk et al. 2015). Moreover, the impact is enhanced when the invader is an ecosystem engineer, belongs to a new functional group or affects the abundance of a keystone species (David et al. 2017). The effects of marine invaders also depend on trophic position and functional similarity. For example, invaders, across studies, typically have negative effects on biodiversity within a trophic level, but positive effects on biodiversity of higher trophic levels (Thomsen et al. 2014). They also can directly or indirectly alter (a)biotic characteristics of ecosystems, resulting in changing energy flows through the food web.

Marenzelleria spp. belong to the 68 most widespread NIS in European Seas (Galil et al. 2014; Cardeccia et al. 2018). In the Baltic Sea, these polychaete worms are amongst the most successful non-native benthic species during recent decades. They were first found there in 1985 and quickly spread throughout the Sea, becoming the dominant species in the zoobenthos of many areas (Blank et al. 2008; Kauppi et al. 2015; Maximov et al. 2015). Studies carried out by both morphological and molecular methods have determined that these polychaetes belong to three related species, *M. viridis* (Verrill), *M. neglecta* Sikorski and Bick and *M. arctia* (Chamberlin) (Sikorski and Bick 2004; Bastrop and Blank 2006; Blank et al. 2008). The first two species came

from North America (Sikorski and Bick 2004). The latter species was previously found only in the Arctic (Jørgensen et al. 1999; Sikorski and Bick 2004). At present, *M. arctia* is prevalent in the deep regions of the northern Baltic Sea (Kauppi et al. 2015; Maximov 2015).

Marenzelleria worms function as ecosystem engineers by modifying the physical, chemical and biological characteristics of bottom sediments (Kristensen et al. 2011; Kauppi et al. 2015; Maximov et al. 2015). The native benthic macrofauna of the northern Baltic Sea is low in diversity and being strongly dominated by a few key species: the bivalve *Macoma balthica* and the crustaceans *Monoporeia affinis* (Lindstrom), *Pontoporeia femorata* Krøyer and *Saduria entomon* (Linnaeus) (Bonsdorff 2006). Indigenous polychaete worms in the northern part of the Baltic Sea are generally few in number and there are no deep-burrowing species amongst them. Invasive polychaetes burrow deeper than local zoobenthos species, causing bioturbation and bioirrigation of bottom sediments. Biological irrigation by *Marenzelleria* spp. promotes deeper penetration of oxygen into sediments and retention of phosphorus in them (Maximov et al. 2015). This, in turn, caused a decrease in the concentration of phosphates in water in some ecosystems of the northern Baltic and contributed to the improvement of the state of the environment by preventing eutrophication and harmful cyanobacterial blooms. However, the effect of oxygenation of bottom sediments becomes significant only at high densities of *Marenzelleria* worms (Berezina et al. 2019). Hence, it is important to forecast changes in the abundance of this species.

It has long been observed that some invaders decline after a period of extremely high abundance (Simberloff and Gibbons 2004). This usually occurs through long-term restructuring of food webs and communities after an invasion and increasing top-down or bottom-up control of invaders (David et al. 2017). Therefore, determining the place that a new invader occupies in the food webs of the recipient's ecosystem is very important. The explosive development of non-indigenous worms *Marenzelleria* occurred in the eastern part of the Gulf of Finland in 2009 after a series of hypoxic – anoxic events that led to the decline of native zoobenthos communities, which were dominated by the amphipod *M. affinis* and the isopod *S. entomon*, over a large area of the Gulf (Maximov 2015). Currently, *M. arctia* dominates the zoobenthos of the easternmost Gulf of Finland (Maximov 2015; Golubkov et al. 2017, 2019).

Stable isotope analysis (SIA) provide new possibilities to investigate aquatic invasion risks and their associated impacts, as it can be an important tool to elucidate the trophic structure and carbon sources in food webs (Middelburg 2014). SIA gives long-term and time-mediated information on consumed trophic resources and is used to describe quantitatively the trophic relationships occurring amongst organisms. SIA can detect potential diet overlap and feeding competition between species and estimating the proportion of different preys and carbon sources in the diet (e.g. Zwerschke et al. 2018; Golubkov et al. 2019; Verstijnen et al. 2019; Golubkov et al. 2020a; Haubrock et al. 2020). Accordingly, it can be used to investigate and predict the impact of invasive species on native ones and on the whole local communities (Haubrock et al. 2020).

The aim of the study was based on 7-year observations to determine the modern trophic position of *M. arctia* in the benthic food webs of the eastern Gulf of Finland in order to assess the prospects for the development of this species in the area. We tested the hypothesis that the dominance and high role of these polychaetes in the benthic macroinvertebrate communities of the Estuary is related to the position of this species in benthic food webs, in which this species is not affected by predators. This goal was attained by performing stable isotope analysis (SIA) of the tissues of zoobenthos and fish. We applied Bayesian mixing model (SIAR; Parnell et al. 2010) to quantify basal resources of various consumers. Outputs from the Bayesian models are in the form of the probability distributions, rather than just summaries of all feasible solutions. As a result of the informative predictions generated by the Bayesian mixing model approach, the SIAR modelling method has become a standard quantitative application for estimating diet resources (Layman et al. 2012; Colborne et al. 2016; Golubkov et al. 2018, 2019).

Materials and methods

Study site and sampling

The Neva Estuary, which is located at the top of the Gulf of Finland (Figure 1), receives water from the Neva River, the most full-flowing river of the Baltic Region, whose flow averages 2492 m^3 s^{-1} (78.6 km^3 $year^{-1}$). It is brackish-water, non-tidal, shallow, with horizontal and vertical gradients of salinity. The morphometric and hydrochemical features of the Neva Estuary have been previously described in many publications (e.g. Golubkov and Alimov 2010; Golubkov and Golubkov 2020).

At present, heavy nutrient and organic matter loading, mainly from the Neva River and St. Petersburg City (the largest megalopolis in the Baltic Region with > 5 million citizens), are the most significant environmental problem for the Neva Estuary. Eutrophication, organic pollution and biological invasions are the most serious threats to the environment of the Neva Estuary (Telesh et al. 2008; Golubkov et al. 2017, 2018, 2020b). NIS have a significant impact on the Estuary environment, many of which have become the dominant species in macroinvertebrate and fish communities over the past two decades (Orlova et al. 2004; Golubkov and Litvinchuk 2015; Maximov 2015; Demchuk et al. 2021).

Samples were collected in the middle part of the Neva Estuary (Figure 1). The salinity of waters near the surface in this part of the Estuary ranges from 1 to 3 PSU and of near bottom waters up to 5 PSU; the depth ranges from 7 m at sampling station 7 and up to 24.5 m at station 5. Zoobenthos was sampled at seven stations (Figure 1) with a modified Van Veen grab (20 × 20 cm) in early August 2014–2020. Samples were sieved in a 0.25 mm mesh with filtered fresh water and preserved in 4% formaldehyde in plastic zip-bags. Large crustacean *S. entomon* (Isopoda) were collected by trawling. Benthic animals for SIA were taken to the laboratory alive. Fish were collected with hook and line and frozen in the laboratory.

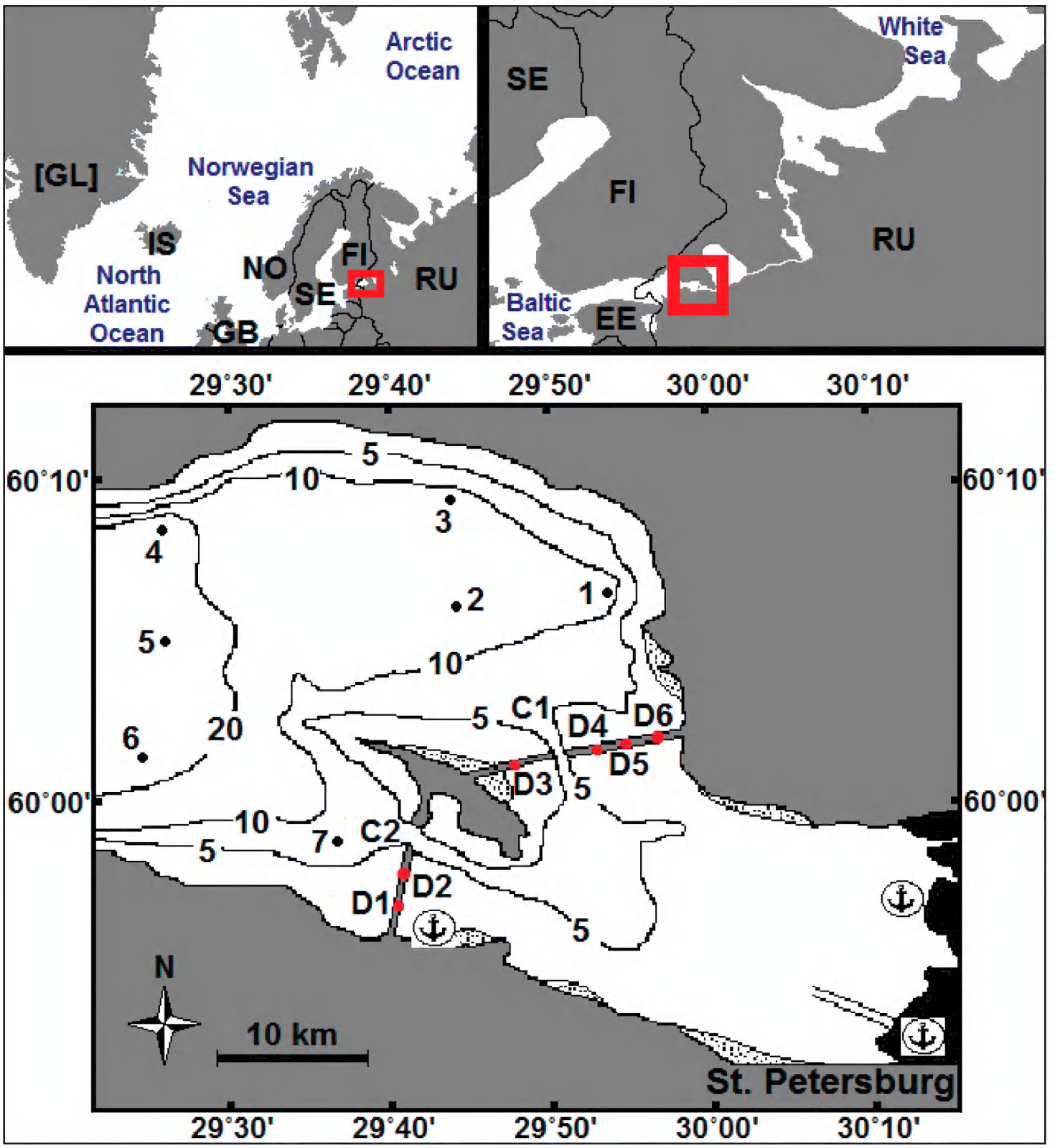

Figure 1. The upper and middle parts of the Neva Estuary with indication of sampling stations (1–7). Black lines: isobaths of 5, 10 and 20 m. Areas with dots indicate dense reeds. C1, C2 – gates for vessels; D1–D6 – waters gates in the St. Petersburg Flood Protection Facility. Anchor marked passenger and cargo ports. Red rectangles – the location of the Neva Estuary. Two-letter country codes are given according to ISO 3166-1 alpha-2 (ISO 2021).

Sample analysis

Invertebrates were picked out of the samples under a stereomicroscope, identified, counted and weighed to the nearest 0.1 mg. Abundance and biomass of animals (wet weight, shells of molluscs included) were estimated as an arithmetic mean ± SEM (standard error of the mean) from seven replicates and re-calculated per 1 m^2 of bottom area.

Live animals for SIA were identified under stereomicroscope and separated by species into vessels containing filtered water. Animals were maintained alive during 2 days

to allow gut clearance. Faecal material was removed periodically to prevent coprophagy. After 2 days, animals were dried at 60 °C for 48 h. Small conspecific individuals were homogenised in an agate mortar to make a composite sample. Samples consisting of muscle tissue were used in the case of large animals (*S. entomon* and fish) as was recommended by Keough et al. (1996). Homogenised animal tissue from composite samples were put into small tin capsules and weighed using a Mettler Toledo MX 5 balance with an accuracy of ± 1 μg. At least three replicates of each type of organism or material were prepared and analysed.

The SIA was performed according to standard methods (Keough et al. 1996) using a Thermo Delta V Plus isotope mass spectrometer (Thermo Scientific, United States) equipped with an element analyser at the Joint Usage Center "Instrumental Methods in Ecology" of the A.N. Severtsov Institute of Ecology and Evolution of RAS (Moscow, Russian Federation). Isotopic composition of C and N in organic matter was expressed in δ-notation relative to the international standard (vPDB for carbon and the atmospheric N_2 for nitrogen): δ (‰) = $(R_{sample}/R_{standard} - 1) \times 1000$, where R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Samples were analysed with reference gas calibrated against IAEA (Vienna, Austria) reference materials USGS 40 and USGS 41. The drift was corrected using an internal laboratory standard (casein). The standard deviation of $\delta^{13}C$ and $\delta^{15}N$ values in the laboratory standard (n = 8) was < 0.2‰. We did not conduct a lipid extraction from animal tissues because it may bias the estimation of trophic links of consumers (Tarroux et al. 2010).

Data modelling

The SIAR v.4.2 package (Parnell and Jackson 2021) running in R Software (version 3.5.1; R Development Core Team 2021; www.r-project.org/) was used for estimating trophic links of the consumers, based on their $\delta^{13}C$ and $\delta^{15}N$ values. SIAR (Stable Isotope Analysis in R) is a mixing model, based on hierarchical Bayesian methods, used to estimate contributions of basal sources, taking into account uncertainty and variability of input data, as well as isotopic enrichment factors (Parnell et al. 2013).

Estimates of the diet of individual organisms were obtained for two-isotope models using the 'SIARsolo' command. The mixing models were run using iterations – 500,000, burn-in – 50,000 and thinning by 15, without using concentration dependencies. Model solutions were presented using credibility intervals (95%, 75%, 25% and 5%) of probability density function distributions (Parnell et al. 2010). To compare the proportions of each source for a group on the boxplots 'siarproportionbygroupplot' command was used. The sensitivity analysis was carried out on fractionation factors as recommended by Inger et al. (2006). Values for trophic fractionation of C and N isotopes were chosen from the C and N range, given in Michener and Kaufman (2007). When an acceptable solution could be found, the simulation results varied by a maximum of 5% for the average contribution to the diet. An acceptable solution was found with trophic enrichment ratios of 1.63‰ for $\delta^{13}C$ and 3.56‰ for $\delta^{15}N$ from Parnell et al. (2013).

Results

Composition and biomass of zoobenthos

Alien polychaete *M. arctia* dominated in the study area during the period of research (Figure 2). *Potamothrix hammoniensis* (Michaelsen) and *Limnodrilus hoffmeisteri* Claparède (Oligochaeta), as well as larvae of *Chironomus plumosus* (Linnaeus) (Diptera, Chironomidae), were subdominant. Indigenous crustacean *S. entomon* (Isopoda) and *M. affinis* (Amphipoda) that dominated in zoobenthos before 2000s (Maximov 2003; Golubkov and Alimov 2010) were rare.

The biomass of polychaete worms significantly decreased in 2014–2020 (Figure 3A). On the contrary, the biomass of oligochaetes showed a positive tendency during this period (Figure 3B). The biomasses of other groups, as well as the total biomass of zoobenthos, did not show any tendencies. Significant negative relationships ($R = -0.44$, $p = 0.002$, $n = 46$) were observed between the biomass of oligochaetes and polychaetes (Figure 4).

Stable isotope analysis and SIAR results

The isotopic signatures of key benthic macroinvertebrates and fish species varied in a wide range, reflecting differences in the use of different resources and in the trophic level (Figure 5).

According to the SIAR modelling, the previously highly dominant invertebrate predator in natural communities, the isopod *S. entomon*, mainly fed on amphipod *M. affinis* and the larvae of *Ch. plumosus* (Figure 6A). *M. affinis* has also been an impor-

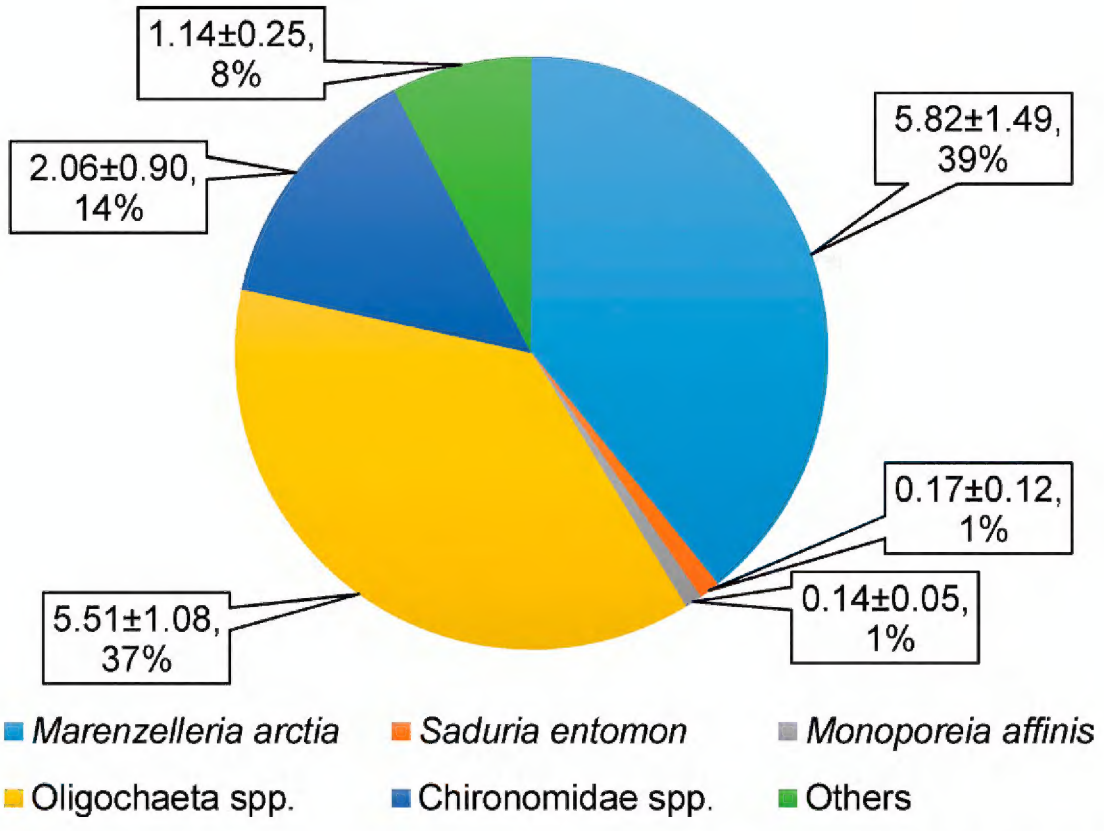

Figure 2. Mean biomass (g WW/m^2) ± the standard error of the mean (SEM) of the dominant zoobenthic groups and their portions (%) in the total biomass of zoobenthos in 2014–2020.

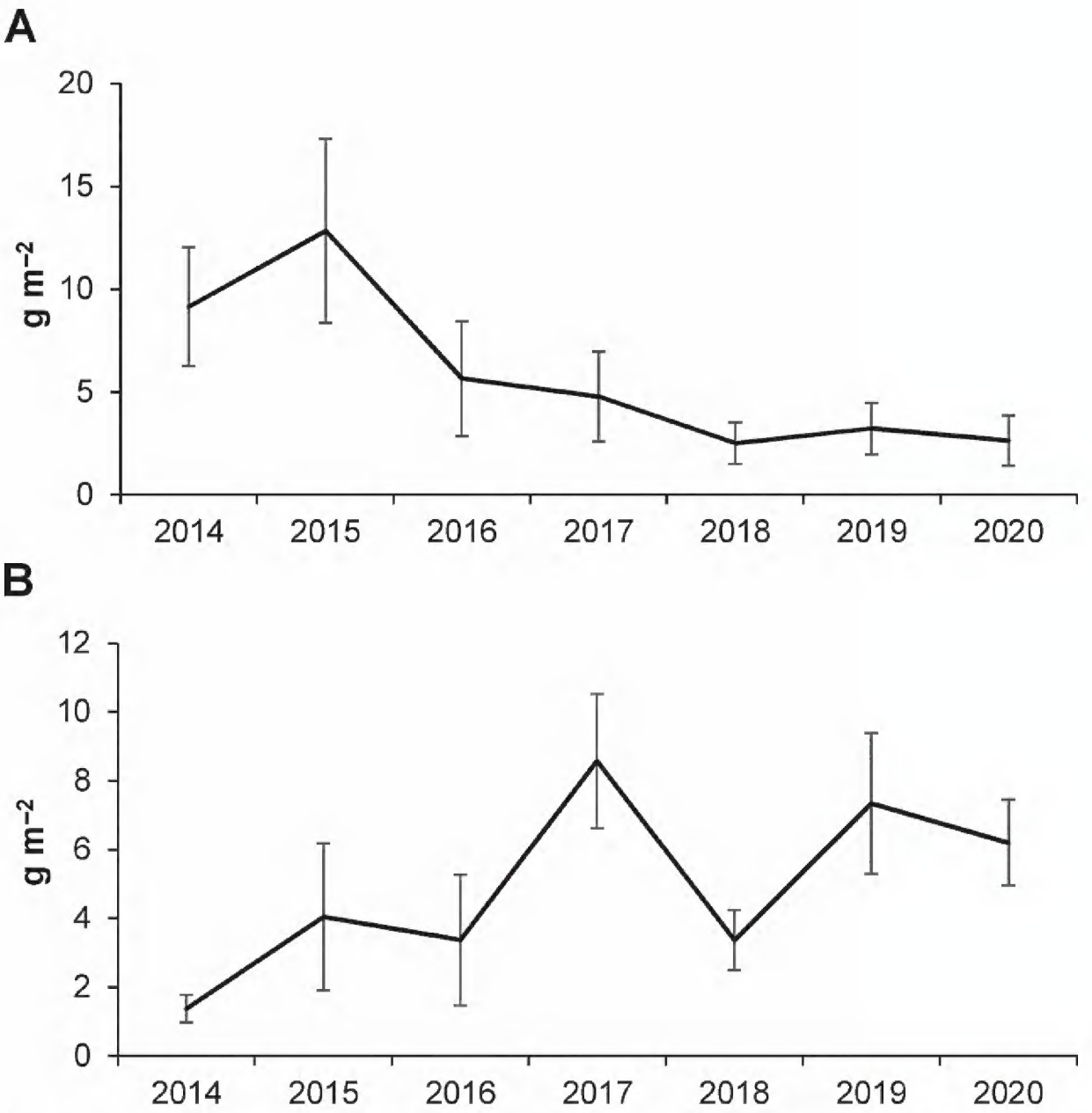

Figure 3. Changes in the biomasses of *Marenzelleria arctia* (**A**) and oligochaetes (**B**) in 2014–2020. Vertical bars are ± SEM.

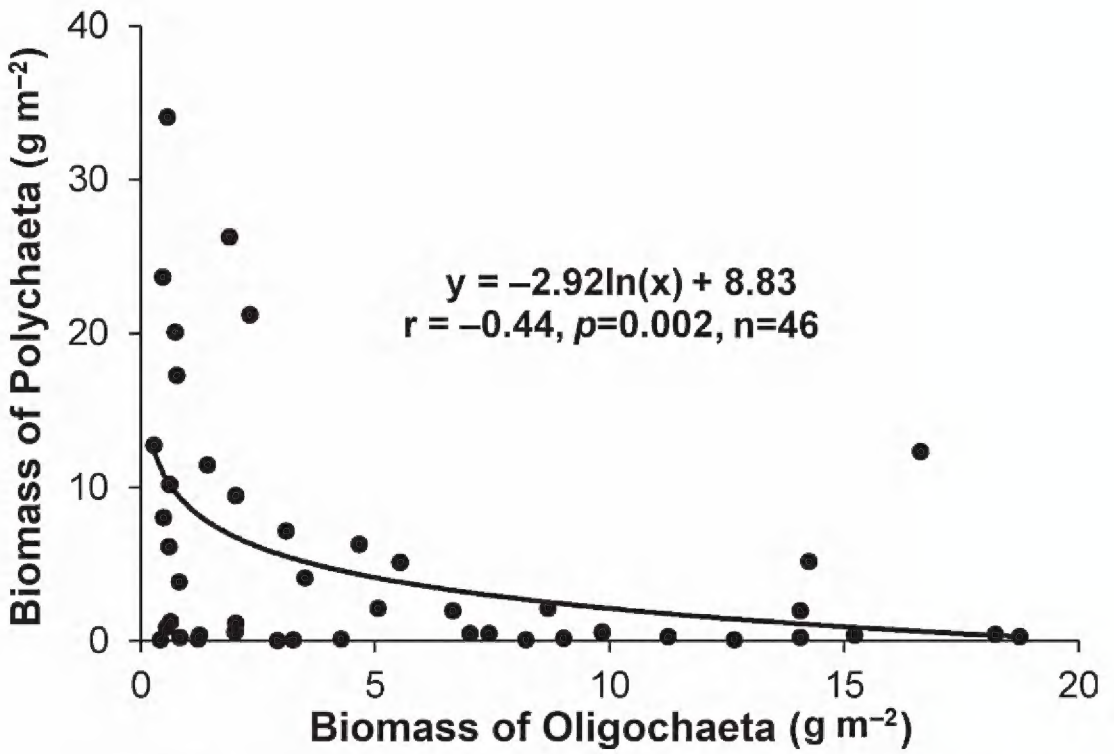

Figure 4. Relationships between the biomass of oligochaetes and polychaetes in the Neva Estuary in 2014–2020.

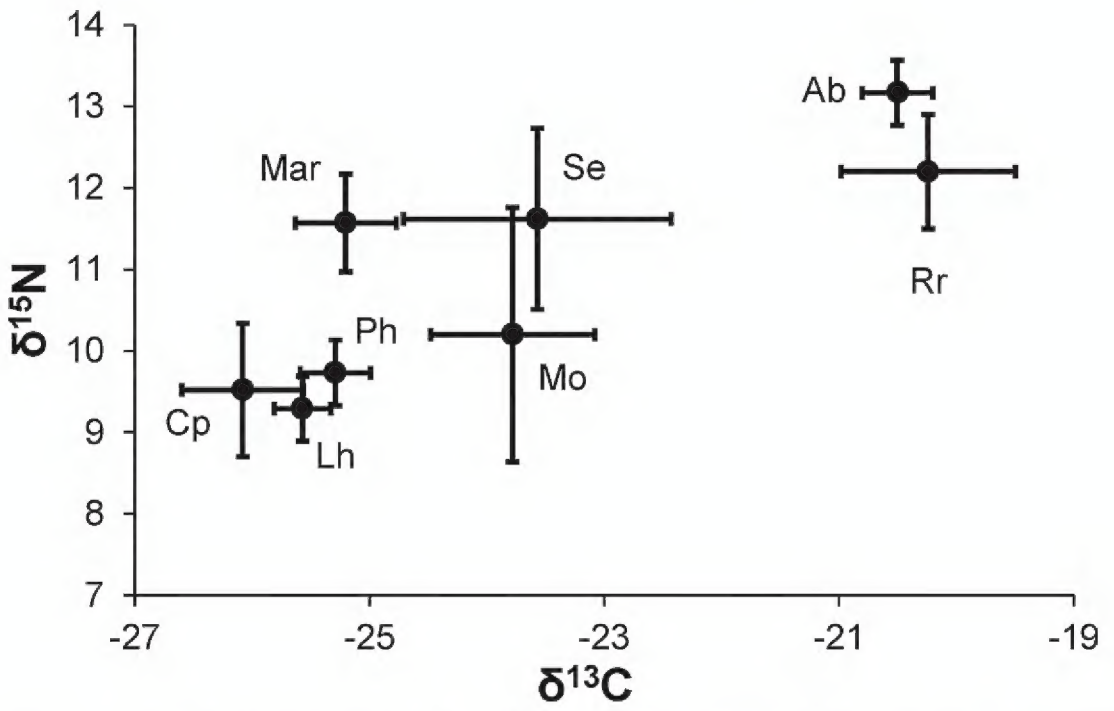

Figure 5. Isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$ values, mean ± SEM) of common zoobenthic species and fish in the Neva Estuary. Cp – *Chironomus plumosus*, Lh – *Limnodrilus hoffmeisteri*, Ph – *Potamothrix hammoniensis*, Mo – *Monoporeia affinis*, Mar – *Marenzelleria arctia*, Se – *Saduria entomon*, Ab – *Abramis brama*, Rr – *Rutilus rutilus*.

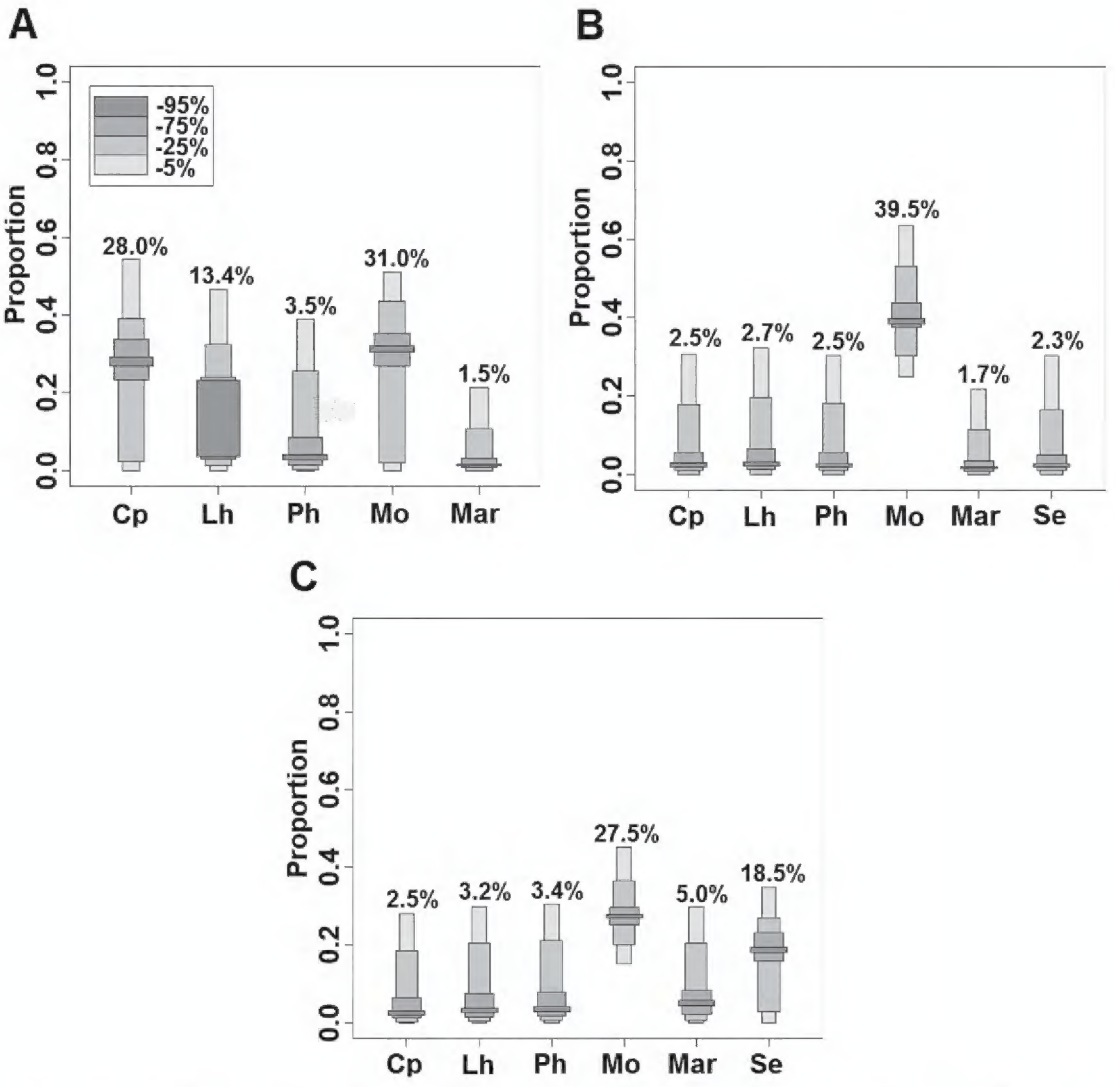

Figure 6. The proportion of the use of various prey by the predatory macroinvertebrate *Saduria entomon* (**A**) and the fish *Rutilus rutilus* (**B**) and *Abramis brama* (**C**) in the Neva Estuary according to the SIAR model. The dark grey, grey, light grey and white are 95%, 75%, 55% and 5% credibility intervals. The numbers indicate the average percentages in the diet for 95% probability. Cp – *Chironomus plumosus*, Lh – *Limnodrilus hoffmeisteri*, Ph – *Potamothrix hammoniensis*, Mo – *Monoporeia affinis*, Mar – *Marenzelleria arctia*, Se – *Saduria entomon*.

tant resource for roach and bream (Figure 6B, C). In turn, *S. entomon*, played a significant role in the feeding of bream (Figure 6C). All of these predators poorly consumed alien polychaetes *M. arctia*, which dominated amongst non-predatory invertebrates.

In accordance with the data on the biomass of consumers and SIA, polychaete worms form the dominant food chain in the food web in the middle part of the Estuary (Figure 7), which apparently plays an important role in energy flow and functioning of the benthic macroinvertebrate community. This food chain is actually a closed branch of the Estuary food webs, since *Marenzelleria* is hardly eaten by secondary consumers. The former dominant food webs, associated with native crustaceans, are now poorly developed.

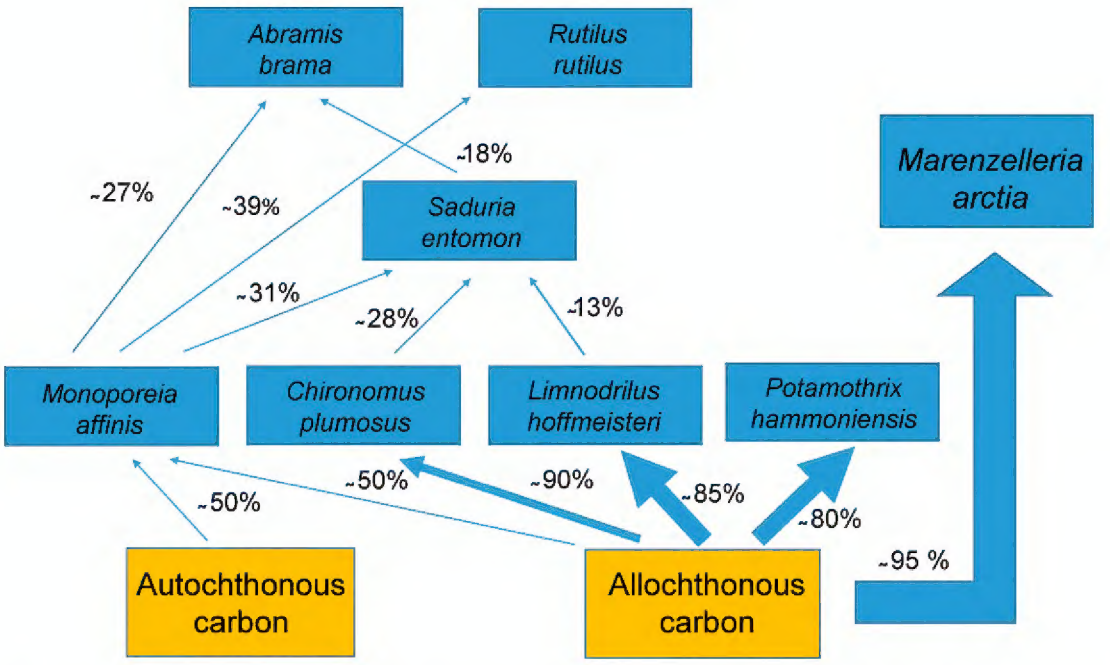

Figure 7. Food web and the share of various carbon resources in the diet of the main consumers in the ecosystem of the Neva Estuary. The use of autochthonous and allochthonous carbon is given according to Golubkov et al. (2019). The thickness of the arrows is proportional to the biomass of consumers.

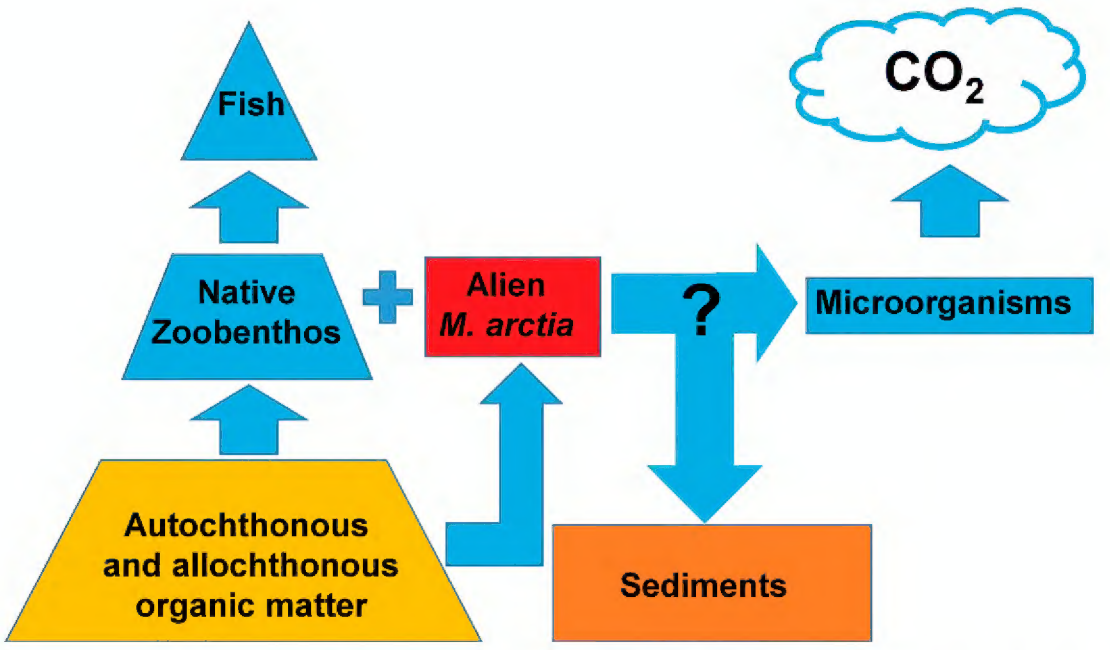

Figure 8. A hypothetical model for the position and functional role of *Marenzelleria arctia* in the bottom food web of the Neva Estuary. Arrows indicate directions of organic matter transfer.

Discussion

Composition and succession of zoobenthos

An important goal of invasion biology is to identify environmental characteristics that may make a region particularly receptive to invasions (David et al. 2017). While some ecologists consider abiotic conditions that are favourable for survival of exotic species (Moyle and Light 1996; Lahdes and Karjala 2007), others focus on their biotic interactions of invaders with native biota (e.g. Ptáčníková et al. 2015; Vanderploeg et al. 2015). Moreover, some studies have shown that if abiotic factors are appropriate for an exotic species, this species is likely to invade successfully, regardless of the native species already present (Moyle and Light 1996; Marchetti et al. 2004; Golubkov et al. 2020b). However, low species and functional diversity also can open an ecosystem for alien species, because unsaturated niche space makes communities more vulnerable for invasions (David et al. 2017). The highest numbers of non-indigenous species were found in the transit water systems in the Baltic Sea: in the Gulf of Finland, the Szczecin Lagoon and the Vistula Lagoon (Zettler et al. 2014). These water systems have wide gradients of environmental characteristics and relatively low species diversity.

Salinity gradient and hypoxia events are the main driving forces of zoobenthic succession in the Baltic Sea area (Rumohr et al. 1996; Bonsdorff 2006; Zettler et al. 2014). Due to low salinity and periodic hypoxia stress, benthic communities in the northern Baltic Sea are species poor and are dominated by few species that currently affect ecosystem functioning (Villnäs et al. 2012). At the same time, freshwater and euryhaline species increase biodiversity in the freshened parts of the Baltic. Amongst them are species that benefit from organic and nutrient enrichment (Balushkina and Golubkov 2018; Golubkov et al. 2019).

All these trends are actual for the zoobenthic community in the middle part of the Neva Estuary. Historical data show that, at the beginning of the last century, benthic communities were rather species-poor and dominated by indigenous crustaceans, *Monoporeia affinis* and *Saduria entomon* (Golubkov and Alimov 2010). Later, due to the increase in organic pollution from St. Petersburg, the oligochaetes, *Potamothrix hammoniensis* and *Limnodrilus hoffmeisteri* and the larvae of *Chironomus plumosus*, which are typical in fresh or slightly brackish polluted waters, also became common. This community existed until the mid-1990s, when, after a series of hypoxic events, the biomass of zoobenthos, especially of hypoxic sensitive crustacean, as well as the energy flow in benthic communities, decreased many times (Golubkov and Alimov 2010; Golubkov et al. 2010; Maximov 2015). The restoration of benthic communities was associated with the development of the alien polychaete *Marenzelleria arctia*, firstly recorded in 2009, which became the dominant species of zoobenthos (Maximov 2011).

When introduced, a species may persist only if it is able to pass through environmental and biotic filters (David et al. 2017). Biotic filters include resource availability, competition with native species and predators. A decrease in the diversity and abundance of communities due to disturbances makes ecosystems less resistant to inva-

sions, since it reduces competition with native species and frees up niche space (Shea and Chesson 2002). The current warming of the climate mainly contributes to the introduction of relatively thermophilic species from middle latitudes to more northern latitudes (e.g. Holopainen et al. 2016). However, in the case of *M. arctia*, the opposite direction of invasions was observed. This species is native to the coastal zone of the Arctic seas, where it is mainly found in river mouths (Sikorski and Buzhinskaya 1998; Sikorski and Bick 2004). It possibly entered the Baltic Sea from the White Sea with the ballast waters of ships through the White Sea-Baltic Canal, which includes a system of lakes and artificial canals (Figure 1). However, the construction of the canal was completed back in 1933. The naturalisation of *M. arctia* in the eastern Gulf of Finland only seven decades later was apparently facilitated by the temporary decline of native zoobenthos species due to hypoxic-anoxic events.

In subsequent years, in 2014–2020, the biomass of *M. arctia* decreased (Figure 3). However, the biomass of benthic crustaceans remained practically unchanged and remained very low. This means that, despite a significant decrease in the invader biomass, the community did not return to its original state and confirms the opinion that, even in those cases where there may be a reasonable expectation of decline, an introduced species can leave a trace long after its influence has weakened (Simberloff and Gibbons 2004). The reason for this may be associated with a change in the configuration of food chains after the introduction of an alien species into the native community.

SIAR modelling and food webs structure

Changes in food web structure following invasion might, in most cases, be mainly related to changes in trophic group abundances rather than to species extinctions, as suggested by a meta-analysis on aquatic ecosystems (Gallardo et al. 2016). The invasion of alien *M. arctia* also did not lead to the extinction of native benthic species. Instead, according to SIA results, it formed its own food chain with low connectivity to the rest of the Estuary food web (Figure 7).

In the Neva Estuary, *M. arctia*, as well as dominant oligochaete and chironomid species, mostly used allochthonous wastewater-derived carbon as a basal resource for their production (Figure 7; Golubkov et al. 2019). Oligochaetes *L. hoffmeisteri* and *P. hammoniensis* (Oligochaeta) and larvae of *Chironomus* spp. are important indicators of polluted waters and benefit from organic pollution (Saether 1979; Rodriguez and Reynoldson 2011). They reach high abundance in the eutrophic and polluted waters of the Baltic Estuaries (Wolnomiejski and Witek 2013; Balushkina and Golubkov 2018; Kornijów et al. 2019; 2021). On the contrary, non-indigenous *M. affinis*, in addition to allochthonous carbon, largely uses autochthonous carbon produced by phytoplankton (Figure 7; Golubkov et al. 2019). This species consumes phytoplankton and phytodetritis, which is deposited on the seabed throughout the Baltic Sea (Lopez and Elmgren 1989; Lehtonen and Andersin 1998).

M. arctia consumes surface sediments and suspension around their burrows (Renz and Forster 2013). Therefore, polychaetes and the amphipods likely compete for food

resources, as both are deposit-feeding animals partly sharing similar food resources (Kotta and Ólafsson 2003). Interspecific and intraspecific competition for food was considered to be the main mechanism regulating the population size of *M. affinis* in the field (Wenngren and Ólafsson 2002; Kotta and Ólafsson 2003). Hence, it can be assumed that the development of the abundant polychaete population after the hypoxia events of the early 2000s prevents the recovery of the *Monoporeia* population. Moreover, an innate tendency of *M. affinis* to move up upon disturbance from burrowing activities of neighbours may result in enhanced susceptibility to predators (Lopez and Elmgren 1989). Thus, the successful competition of *Marenzelleria* with *Monoporeia* may be facilitated by the fact that the population of the latter, unlike polychaetes, is under the influence of *S. entomon* and fish (Figure 7).

It has often been observed that NIS populations decline after an initial period of high abundance (David et al. 2017). In the Neva Estuary, we also observed a progressive decline of *M. arctia* biomass during 2014–2020 (Figure 3A). Significant negative relationships were found between the biomass of oligochaetes and polychaetes in the Estuary (Figure 4). The reason may lie in interspecific competition for resources between polychaetes and oligochaetes, since both groups mainly use allochthonous carbon for their production (Figure 7; Golubkov et al. 2019). However, consuming organic matter from different layers of sediment can prevent food competition (Kornijów et al. 2021). *L. hoffmeisteri* and *P. hammoniensis* (Tubificinae, Oligochaeta) ingest food particles from deep sediment layers and defecate faeces at the sediment surface (Davis 1974; Rodriguez and Reynoldson 2011; Kornijów et al. 2021), while *Marenzelleria* spp. collect particles at the surface around burrows and defecate faeces deep into sediments (Renz and Forster 2013). Therefore, the activity of worms of these zoobenthic groups causes differently directed fluxes in bottom sediments. The bioturbation activity of polychaetes causes the transport of solid and dissolved organic matter from the surface to the deep layers of bottom sediments. They enrich the deep sediment layers with organic matter and stimulate microbial particles reworking in them (Renz and Forster 2013). On the contrary, the bioturbation activity of oligochaetes causes an upward transfer of old-age substances contained deep in bottom sediments, which reduces the content of organic matter on their surface (Davis 1974; Kornijów et al. 2021). Accordingly, this upward conveyor can negatively affect the feeding conditions of *M. arctia* if the oligochaete biomass increases. On the other hand, this can hardly lead to the complete elimination of *Marenzelleria* from the system, due to the sedimentation of phytoplankton and other organic particles from the water column. Most likely, this should help stabilise the biomass of polychaetes at some equilibrium level.

SIAR modelling showed that the main invertebrate predator, *S. entomon* and fishes do not feed on *M. arctia*. As a result, the food chain leading to polychaete worms practically does not interact with other food chains of the benthic food web (Figure 7). The probable reason is that *Marenzelleria* spp. burrow deep into bottom sediments (Renz and Forster 2013). Their burrows probably allow these species to effectively avoid predation by surface invertebrate predators and fish. Instead, surface-dwelling

amphipod *M. affinis* is a preferred food item for *Saduria* (Ejdung and Elmgren 2001). This crustacean is also a favourite food of fish in the Neva Estuary (Kudersky et al. 2007). Subsurface-dwelling larvae of *Ch. plumosus* and burrowing oligochaetes are less important sources of carbon for secondary consumers (Figures 6, 7). The vertical distribution of zoobenthos is an important trait of its suitability for benthic-feeding fish (e.g. Moss and Timms 1989; Persson and Svensson 2006; Weigel and Bonsdorff 2018). In an estuary of the southern Baltic, the Darss-Zingster Bodden Chain, the only recognisable remains of *M. viridis* in bream, carp and flounder were the bristles (Winkler and Debus 1996). These were usually taken in with detritus. Whole *Marenzelleria* in the guts of these fish were never found. However, they have been found in small numbers in the guts of pikeperch. It probably consumed polychaetes during their nocturnal migration into the water column (Winkler and Debus 1996).

A hypothetical model for the position and functional role of *M. arctia* in the bottom food web is given in Figure 8. The invasion of *M. arctia* has created a new offshoot in the estuarine food webs. The lack of the top-down control obviously contributes to significant development of this food chain. Unlike native food webs, this food chain does not provide energy transfer from autochthonous and allochthonous organic matter to the upper trophic levels and obviously negatively affects demersal fish production. This means that NIS can not only fill in the free nodes in food webs, but also reconstruct food chains, diverting resources that were previously consumed by other species and directing them along chains that are not always useful for humans. On the other hand, earlier there were no burrowing polychaetes in the Neva Estuary and the invasion of *Marenzelleria* formed a new functional group in its ecosystem (Maximov et al. 2015). Their activity leads to bioturbation and bioirrigation of bottom sediments and stimulates the decomposition of organic matter by worms and microorganisms (Figure 8). However, all these processes deserve further detailed research.

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References

Balushkina EV, Golubkov SM (2018) Water quality and biodiversity of benthic animals in the Neva Estuary under anthropogenic stress. Fundamentalnaya i Prikladnaya Gidrofizika 11: 51–61. https://doi.org/10.7868/S2073667318020041

Bastrop R, Blank M (2006) Multiple invasions – a polychaete genus enters the Baltic Sea. Biological Invasions 8: 1195–1200. https://doi.org/10.1007/s10530-005-6186-6

Berezina NA, Maximov AA, Vladimirova OM (2019) Influence of benthic invertebrates on phosphorus flux at the sediment-water interface in the easternmost Baltic Sea. Marine Ecology Progress Series 608: 33–43. https://doi.org/10.3354/meps12824

Blank M, Laine AO, Jürss K, Bastrop R (2008) Molecular identification key based on PCR/RFLP for three polychaete sibling species of the genus *Marenzelleria*, and the species' current distribution in the Baltic Sea. Helgoland Marine Research 62: 129–141. https://doi.org/10.1007/s10152-007-0081-8

Bonsdorff E (2006) Zoobenthic diversity-gradients in the Baltic Sea: continuous post-glacial succession in a stressed ecosystem. Journal of Experimental Marine Biology and Ecology 330: 383–391. https://doi.org/10.1016/j.jembe.2005.12.041

Cardeccia A, Marchini A, Occhipinti-Ambrogi A, Galil B, Gollasch S, Minchin D, Narščius A, Olenin S, Ojaveer H (2018) Assessing biological invasions in European Seas: Biological traits of the most widespread non-indigenous species. Estuarine, Coastal and Shelf Science 201: 17–28. https://doi.org/10.1016/j.ecss.2016.02.014

Colborne SF, Rush SA, Paterson G, Johnson TB, Lantry BF, Fisk AT (2016) Estimates of lake trout (*Salvelinus namaycush*) diet in Lake Ontario using two and three isotope mixing models. Journal of Great Lakes Research 42: 695–702. https://doi.org/10.1016/j.jglr.2016.03.010

David P, Thébault E, Anneville O, Duyck P-F, Chapuis E, Loeuille N (2017) Chapter One – Impacts of invasive species on food webs: A review of empirical data. Advances in Ecological Research 56: 1–60. https://doi.org/10.1016/bs.aecr.2016.10.001

Davis RB (1974) Stratigraphic effects of tubificids in profundal lake sediments. Limnology and Oceanography 19: 466–488. https://doi.org/10.4319/lo.1974.19.3.0466

Demchuk AS, Uspenskiy AA, Golubkov SM (2021) Abundance and feeding of fish in the coastal zone of the Neva Estuary, eastern Gulf of Finland. Boreal Environment Research 26: 1–16.

Ejdung G, Elmgren R (2001) Predation by the benthic isopod *Saduria entomon* on two Baltic Sea deposit-feeders, the amphipod *Monoporeia affinis* and the bivalve *Macoma balthica*. Journal of Experimental Marine Biology and Ecology 266: 165–179. https://doi.org/10.1016/S0022-0981(01)00353-7

Galil BS, Marchini A, Occhipinti-Ambrogi A, Minchin D, Narščius A, Ojaveer H, Olenin S (2014) International arrivals: widespread bioinvasions in European Seas. Ethology Ecology & Evolution 26(2–3): 152–171. https://doi.org/10.1080/03949370.2014.897651

Gallardo B, Clavero M, Sánchez MI, Vilà M (2016) Global ecological impacts of invasive species in aquatic ecosystems. Global Change Biology 22: 151–163. https://doi.org/10.1111/gcb.13004

Golubkov M, Golubkov S (2020) Eutrophication in the Neva Estuary (Baltic Sea): response to temperature and precipitation patterns. Marine and Freshwater Research 71: 583–595. https://doi.org/10.1071/MF18422

Golubkov MS, Nikulina VN, Tiunov AV, Golubkov SM (2020a) Stable C and N isotope composition of suspended particulate organic matter in the Neva Estuary: the role of abiotic

factors, productivity, and phytoplankton taxonomic composition. Journal of Marine Science and Engineering 8(12): e959. https://doi.org/10.3390/jmse8120959

Golubkov MS, Litvinchuk LF, Golubkov SM (2020) Effects of environmental gradients on the biomass of alien *Cercopagis pengoi* in the Neva Estuary. Frontiers in Marine Science 7: e573289. https://doi.org/10.3389/fmars.2020.573289

Golubkov SM (2021) Effect of climatic fluctuations on the structure and functioning of ecosystems of continental water bodies. Contemporary Problems of Ecology 14(1): 1–10. https://doi.org/10.1134/S1995425521010030

Golubkov S, Alimov A (2010) Ecosystem changes in the Neva Estuary (Baltic Sea): natural dynamics or response to anthropogenic impacts? Marine Pollution Bulletin 61: 198–204. https://doi.org/10.1016/j.marpolbul.2010.02.014

Golubkov SM, Maximov AA, Golubkov MS, Litvinchuk LF (2010). A functional shift in the ecosystem of the eastern Gulf of Finland caused by natural and anthropogenic factors. Doklady Biological Sciences 432: 198–200. https://doi.org/10.1134/S0012496610030099

Golubkov SM, Litvinchuk LF (2015) The role of the alien species *Cercopagis pengoi* in zooplankton of the Eastern Gulf of Finland of the Baltic Sea. Doklady Biological Science 462: 121–123. https://doi.org/10.1134/S0012496615030011

Golubkov S, Golubkov M, Tiunov A, Nikulina L (2017) Long-term changes in primary production and mineralization of organic matter in the Neva Estuary (Baltic Sea). Journal of Marine Systems 171: 73–80. https://doi.org/10.1016/j.jmarsys.2016.12.009

Golubkov SM, Berezina NA, Gubelit YI, Demchuk AS, Golubkov MS, Tiunov AV (2018) A relative contribution of carbon from green tide algae *Cladophora glomerata* and *Ulva intestinalis* in the coastal food webs in the Neva Estuary (Baltic Sea). Marine Pollution Bulletin 126: 43–50. https://doi.org/10.1016/j.marpolbul.2017.10.032

Golubkov SM, Golubkov MS, Tiunov AV (2019) Anthropogenic carbon as a basal resource in the benthic food webs in the Neva Estuary (Baltic Sea). Marine Pollution Bulletin 146: 190–200. https://doi.org/10.1016/j.marpolbul.2019.06.037

Haubrock PJ, Balzani P, Britton JR, Haase P (2020) Using stable isotopes to analyse extinction risks and reintroduction opportunities of native species in invaded ecosystems. Scientific Reports 10: e21576. https://doi.org/10.1038/s41598-020-78328-9

Holopainen R, Lehtiniemi M, Meier HEM, Albertsson J, Gorokhova E, Kotta J, Viitasalo M (2016) Impacts of changing climate on the non-indigenous invertebrates in the northern Baltic Sea by end of the twenty-first century. Biological Invasions 18: 3015–3032. https://doi.org/10.1007/s10530-016-1197-z

International Organization for Standardization (ISO) (2021) Country Codes – ISO 3166. https://www.iso.org/iso-3166-country-codes.html

Inger R, Ruxton G D, Newton J, Colhoun K, Robinson JA, Jackson AL, Bearhop S (2006) Temporal and intrapopulation variation in prey choice of wintering geese determined by stable isotope analysis. Journal of Animal Ecology 75: 1190–1200. https://doi.org/10.1111/j.1365-2656.2006.01142.x

Jørgensen LL, Pearson TH, Anisimova NA, Gulliksen B, Dahle S, Denisenko SG, Matishov GG (1999) Environmental influences on benthic fauna associations of the Kara Sea (Arctic Russia). Polar Biology 22: 395–416. https://doi.org/10.1007/s003000050435

Kauppi L, Norkko A, Norkko J (2015) Large-scale species invasion into a low-diversity system: spatial and temporal distribution of the invasive polychaetes *Marenzelleria* spp. in the Baltic Sea. Biological Invasions 17: 2055–2074. https://doi.org/10.1007/s10530-015-0860-0

Keough JR, Sierszen ME, Hagley CA (1996) Analysis of a Lake Superior coastal food web with stable isotope techniques. Limnology and Oceanography 14: 136–146. https://doi.org/10.4319/lo.1996.41.1.0136

Kornijów R, Markiyanova M, Lange E (2019) Feeding by two closely related species of *Chironomus* (Diptera: Chironomidae) in south Baltic lagoons, with implications for competitive interactions and resource partitioning. Aquatic Ecology 53: 315–324. https://doi.org/10.1007/s10452-019-09691-7

Kornijów R, Pawlikowski K, Błędzki LA, Drgas A, Piwosz K, Ameryk A, Całkiewicz J (2021) Co-occurrence of oligochaetes and chironomid larvae in soft sediments with potential resource partitioning. Aquatic Sciences 83: e51. https://doi.org/10.1007/s00027-021-00800-z

Kotta J, Ólafsson E (2003) Competition for food between the introduced polychaete *Marenzelleria viridis* (Verrill) and the native amphipod *Monoporeia affinis* Lindström in the Baltic Sea. Journal of Sea Research 50: 27–35. https://doi.org/10.1016/S1385-1101(03)00041-8

Kristensen E, Hansen T, Delefosse M, Banta GT, Quintana CO (2011) Contrasting effects of the polychaetes *Marenzelleria viridis* and *Nereis diversicolor* on benthic metabolism and solute transport in sandy coastal sediment. Marine Ecology Progress Series 425: 125–139. https://doi.org/10.3354/meps09007

Kudersky LA, Churukhin AS, Popov AP, Bogdanov DV, Yakovlev AS (2008) Fish population of the Neva Estuary. In: Alimov AF, Golubkov SM (Eds) Biodiversity and Ecological Problems of the Neva Estuary. KMK Publishers, Moscow, 223–240. [In Russian]

Kumschick S, Bacher S, Dawson W, Heikkilä J, Sendek A, Pluess T, Robinson TB, Kühn I (2012) A conceptual framework for prioritization of invasive alien species for management according to their impact. NeoBiota 15: 69–100. https://doi.org/10.3897/neobiota.15.3323

Kumschick S, Gaertner M, Vilà M, Essl F, Jeschke JM, Pyšek P, Ricciardi A, Bacher S, Blackburn TM, Dick JTA, Evans T, Hulme PE, Kühn I, Mrugała A, Pergl J, Rabitsch W, Richardson DM, Sendek A, Winter M (2015) Ecological impacts of alien species: quantification, scope, caveats, and recommendations. BioScience 65: 55–63. https://doi.org/10.1093/biosci/biu193

Kumschick S, Wilson JRU, Foxcroft LC (2020) A framework to support alien species regulation: the Risk Analysis for Alien Taxa (RAAT). In: Wilson JR, Bacher S, Daehler CC, Groom QJ, Kumschick S, Lockwood JL, Robinson TB, Zengeya TA, Richardson DM (Eds) Frameworks used in Invasion Science. NeoBiota 62: 213–239. https://doi.org/10.3897/neobiota.62.51031

Lahdes EO, Karjala LA (2007) Implications of water ionic composition for invasion of euryhaline species in inland waters – an experimental study with *Cercopagis pengoi* from the northern Baltic Sea. Aquatic Invasions 2: 422–430. https://doi.org/10.3391/ai.2007.2.4.12

Layman CA, Araujo MS, Boucek R, Hammerschlag-Peyer CM, Harrison E, Jud ZR, Matich P, Rosenblatt AE, Vaudo JJ, Yeager LA, Post DM, Bearhop S (2012) Applying stable isotopes to examine food-web structure: an overview of analytical tools. Biological Reviews 87: 545–562. https://doi.org/10.1111/j.1469-185X.2011.00208.x

Lehtiniemi M, Ojaveer H, David M, Galil BS, Gollasch S, McKenzie C, Minchin D, Occhipinti-Ambrogi A, Olenin S, Pederson J (2015) Dose of truth – Monitoring marine non-indigenous species to serve legislative requirements. Marine Policy 54: 26–35. https://doi.org/10.1016/j.marpol.2014.12.015

Lehtonen K, Andersin A-B (1998) Population dynamics, response to sedimentation and role in benthic metabolism of the amphipod *Monoporeia affinis* in an open-sea area of the northern Baltic Sea. Marine Ecology Progress Series 168: 71–85. https://doi.org/10.3354/meps168071

Lopez G, Elmgren R (1989) Feeding depths and organic absorption for the deposit feeding amphipods *Pontoporeia affinis* and *P. femorata*. Limnology and Oceanography 34: 982–991. https://doi.org/10.4319/lo.1989.34.6.0982

Marchetti MP, Moyle PB, Levine R (2004) Alien fishes in California watersheds: characteristics of successful and failed invaders. Ecological Applications 14: 587–596. https://doi.org/10.1890/02-5301

Maximov AA (2003) Changes of the bottom macrofauna in the eastern Gulf of Finland in 1985–2002. Proceedings of the Estonian Academy of Sciences. Biology. Ecology 52(4): 378–393.

Maximov AA (2011) Large-scale invasion of *Marenzelleria* spp. (Polychaeta; Spionidae) in the eastern Gulf of Finland, Baltic Sea. Russian Journal of Biological Invasions 2(1): 11–19. https://doi.org/10.1134/S2075111711010036

Maximov A (2015) The long-term dynamics and current distribution of macrozoobenthos communities in the eastern Gulf of Finland, Baltic Sea. Russian Journal of Marine Biology 41(4): 300–310. https://doi.org/10.1134/S1063074015040094

Maximov A, Bonsdorff E, Eremina T, Kauppi L, Norkko A, Norkko J (2015) Context-dependent consequences of *Marenzelleria* spp. (Spionidae: Polychaeta) invasion for nutrient cycling in the northern Baltic Sea. Oceanologia 57(4): 342–348. https://doi.org/10.1016/j.oceano.2015.06.002

Michener RH, Kaufman L (2007) Stable isotope ratios as tracers in marine food webs: an update. In: Michener R, Lajtha K (Eds) Stable Isotopes in Ecology and Environmental Science, second ed. Blackwell Publishing Ltd, Oxford, 238–282. https://doi.org/10.1002/9780470691854

Middelburg JJ (2014) Stable isotopes dissect aquatic food webs from the top to the bottom. Biogeosciences 11: 2357–2371. https://doi.org/10.5194/bg-11-2357-2014

Moyle PB, Light T (1996) Fish invasions in California: do abiotic factors determine success? Ecology 77: 1666–1670. https://doi.org/10.2307/2265770

Moritz C, Agudo R (2013) The future of species under climate change: Resilience or decline? Science 341: 504–508. https://doi.org/10.1126/science.1237190

Moss B, Timms M (1989) Predation, sediment stability and food availability as determinants of the benthic invertebrate fauna in two shallow lakes. Hydrobiologia 185: 249–257. https://doi.org/10.1007/BF00036613

Ojaveer H, Galil BS, Campbell ML, Carlton JT, Canning-Clode J, Cook EJ, Davidson AD, Hewitt CL, Jelmert A, Marchini A, McKenzie CH, Minchin D, Occhipinti-Ambrogi A, Olenin S, Ruiz G (2015) Classification of non-indigenous species based on their impacts:

Considerations for application in marine management. PLoS Biology 13(4): e1002130. https://doi.org/10.1371/journal.pbio.1002130

Orlova M, Golubkov S, Kalinina L, Ignatieva N (2004) *Dreissena polymorpha* (Bivalvia: Dreissenidae) in the Neva Estuary (eastern Gulf of Finland, Baltic Sea): Is it a biofilter or source for pollution? Marine Pollution Bulletin 49: 196–205. https://doi.org/10.1016/j.marpolbul.2004.02.008

Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: coping with too much variation. PLoS ONE 5: e9672. https://doi.org/10.1371/journal.pone.0009672

Parnell AC, Jackson AL (2021) siar: Stable Isotope Analysis in R (version 4.2). [software]. https://cran.r-project.org/web/packages/siar/index.html

Parnell AC, Philips DL, Bearshop S, Semmens BX, Ward EJ, Moore JW, Inger R (2013) Bayesian stable isotope mixing models. Environmetrics 24: 387–399. https://doi.org/10.1002/env.2221

Penk M, Irvine K, Donohue I (2015) Ecosystem-level effects of a globally spreading invertebrate invader are not moderated by a functionally similar native. Journal of Animal Ecology 84(6): 1628–1636. https://doi.org/10.1111/1365-2656.12402

Persson A, Svensson JM (2006) Vertical distribution of benthic community responses to fish predators, and effects on algae and suspended material. Aquatic Ecology 40: 85–95. https://doi.org/10.1007/s10452-005-9014-2

Ptáčníková R, Vanderploeg HA, Cavaletto JF (2015) Big versus small: Does *Bythotrephes longimanus* predation regulate spatial distribution of another invasive predatory cladoceran, *Cercopagis pengoi*? Journal of Great Lakes Research 41: 143–149. https://doi.org/10.1016/j.jglr.2015.10.006

R Development Core Team (2021) The R project for statistical computing (version 3.5.1) [software]. http://www.r-project.org

Renz JR, Forster S (2013) Are similar worms different? A comparative tracer study on bioturbation in the three sibling species *Marenzelleria arctia*, *M. viridis*, and *M. neglecta* from the Baltic Sea. Limnology and Oceanography 58(6): 2046–2058. https://doi.org/10.4319/lo.2013.58.6.2046

Rodriguez P, Reynoldson TB (2011) The Pollution Biology of Aquatic Oligochaetes. Springer, London, 265 pp. https://doi.org/10.1007/978-94-007-1718-3

Rumohr H, Bonsdorff E, Pearson TH (1996) Zoobenthic succession in Baltic sedimentary habitats. Archive of Fishery and Marine Research 44: 179–214.

Saether OA (1979) Chironomid communities as water quality indicators. Ecography 2(2): 65–74. https://doi.org/10.1111/j.1600-0587.1979.tb00683.x

Sikorski AV, Buzhinskaya GN (1998) The genus Marenzelleria (Polychaeta, Spionidae) in seas of Russia. Zoologicheskii Zhurnal 77(10): 1111–1120. [In Russian]

Sikorski AV, Bick A (2004) Revision of *Marenzelleria* Mesnil, 1896 (Spionidae, Polychaeta). Sarsia 89(4): 253–275. https://doi.org/10.1080/00364820410002460

Simberloff D, Gibbons L (2004) Now you see them, now you don't! – Population crashes of established introduced species. Biological Invasions 6: 161–172. https://doi.org/10.1023/B:BINV.0000022133.49752.46

Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. Trends in Ecology and Evolution 17(4): 170–176. https://doi.org/10.1016/S0169-5347(02)02495-3

Tarroux A, Ehrich D, Lecomte N, Jardine TD, Bety J, Berteaux D (2010) Sensitivity of stable isotope mixing models to variation in isotopic ratios: evaluating consequences of lipid extraction: lipid extraction in isotopic analysis. Methods in Ecology and Evolution 1: 231–241. https://doi.org/10.1111/j.2041-210X.2010.00033.x

Telesh IV, Golubkov SM, Alimov AF (2008) The Neva Estuary ecosystem. In: Schiewer U (Ed.) Ecology of Baltic Coastal Waters. Ecological Studies 197. Springer-Verlag, Berlin, 259–284. https://doi.org/10.1007/978-3-540-73524-3

Thomsen MS, Byers JE, Schiel DR, Bruno JF, Olden JD, Wernberg T, Silliman BR (2014) Impacts of marine invaders on biodiversity depend on trophic position and functional similarity. Marine Ecology Progress Series 495: 39–47. https://doi.org/10.3354/meps10566

Vanderploeg HA, Pothoven SA, Krueger D, Mason DM, Liebig JR, Cavaletto JF, Ruberg SA, Lang GA, Ptáčníková R (2015) Spatial and predatory interactions of visually preying nonindigenous zooplankton and fish in Lake Michigan during midsummer. Journal of Great Lakes Research 41: 125–142. https://doi.org/10.1016/j.jglr.2015.10.005

Verstijnen YJM, Lucassen ECHET, van der Gaag M, Wagenvoort AJ, Castelijns H, Ketelaars HAM, van der Velde G, Smolders AJP (2019) Trophic relationships in Dutch reservoirs recently invaded by Ponto-Caspian species: insights from fish trends and stable isotope analysis. Aquatic Invasions 14(2): 280–298. https://doi.org/10.3391/ai.2019.14.2.08

Villnäs A, Norkko J, Lukkari K, Hewitt J, Norkko A (2012) Consequences of increasing hypoxic disturbance on benthic communities and ecosystem functioning. PLoS ONE 7(10): e44920. https://doi.org/10.1371/journal.pone.0044920

Weigel B, Bonsdorff E (2018) Trait-based predation suitability offers insight into effects of changing prey communities. PeerJ 6: e5899. https://doi.org/10.7717/peerj.5899

Wenngren J, Ólafsson E (2002) Intraspecific competition for food within and between year-classes in the deposit feeding amphipod *Monoporeia affinis* – the cause of population fluctuations? Marine Ecology Progress Series 240: 205–213. https://doi.org/10.3354/meps240205

Winkler HM, Debus L (1996) Is the polychaete *Marenzelleria viridis* an important food item for fish? Proceedings of the 13th Symposium of the Baltic Marine Biologists: 147–151.

Wolnomiejski N, Witek Z (2013) Szczecin Lagoon Ecosystem: the Biotic Community of the Great Lagoon and its Food Web Model. Versita, London, 231 pp. https://doi.org/10.2478/9788376560502

Zettler ML, Karlsson A, Kontula T, Gruszka P, Laine AO, Herku K, Schiele KS, Maximov A, Haldin J (2014) Biodiversity gradient in the Baltic Sea: a comprehensive inventory of macrozoobenthos data. Helgoland Marine Research 68: 49–57. https://doi.org/10.1007/s10152-013-0368-x

Zwerschke N, van Rein H, Harrod C, Reddin C, Emmerson MC, Roberts D, O'Connor NE (2018) Competition between co-occurring invasive and native consumers switches between habitats. Functional Ecology 32: 2717–2729. https://doi.org/10.1111/1365-2435.13211